TAXONOMIC IMPLICATIONS OF ANEUPLOIDY AND POLYPLOIDY IN *POTAMOGETON* (POTAMOGETONACEAE)

DONALD H. LES

ABSTRACT

A synoptic study of chromosome number reports for 73 species of *Potamogeton* presents evidence supporting the conclusion that the genus is characterized by two different polyploid lineages (one based upon $x = 7$ and the other upon $x = 13$). Analyzed comparatively, chromosome numbers also indicate that the diploid level of the genus is $2n = 14$, and that the $x = 13$ lineage arose by aneuploidy from a $2n = 14$ progenitor. Comparisons developed by juxtaposition of chromosome numbers with morphological characters and classification ranks indicate that subsections *Pusilli*, *Oxyphylli*, and *Amplifolii* may not represent entirely natural assemblages. The past use of chromosome numbers to demonstrate the primitiveness of submersed leaves in the genus is challenged due to lack of correlation of these features when a larger number of species is considered. Chromosome numbers were found to correlate geographically with the hypothetically proposed birthplace of the genus.

Potamogeton is a large (ca. 100 species) and diverse genus of strictly aquatic monocotyledons (Cook, et al., 1974). Morphological diversity in *Potamogeton* is extensive, with many of the species exhibiting heterophylly (producing both floating and submersed foliage), whereas other species possess only leaves which are entirely submersed. Researchers have often recognized two morphological groups within subgenus *Potamogeton* (*Eupotamogeton* Raunk.): the "linear-leaved" species (*e.g.*, Fernald, 1932) and the "broad-leaved" species (*e.g.*, Ogden, 1943). Both linear and broad-leaved species occur within several different subsections, thus neither group has been taxonomically well-defined. Considerably diversity within the genus is also apparent by the variety of fruit and stipule characters found among the species. *Potamogeton* is also characterized by a complex array of polyploidy which has not yet been given a thorough systematic evaluation.

While no generally acceptable classification has been developed for *Potamogeton*, taxonomists have relied for nearly 70 years upon the one developed by Hagström (1916). It has undergone only slight modifications (by St. John, 1916; Fernald, 1932; Ogden, 1943; Haynes, 1974; and others) in only portions of the genus. Hagström's classification has been criticized on several occasions for its unwieldy nature. It included 2 subgenera, 5 sections, 26 subsections,

138 species and multitudes of series, subseries, varieties, forms, and hybrids, yet neither a key to nor a synopsis of any of the ranks were given. St. John (1925, p. 462) emphasized this and stated, "There is no key of any kind. In order to identify a *Potamogeton*, it is necessary to read every page of this work, and practically memorize them." There was no critique that the ranks in the classification were not unified by a phylogenetic framework, therefore, although similar taxa were grouped together, there was little indication of overall relationships among the groups. Hagström approached classification of *Potamogeton* anatomically, largely following Raunkiaer's (1895–99) precedent. This approach was quite different from the morphologically oriented one used by Ascherson and Graebner (1907) to construct an earlier classification. Fernald (1932) later deemphasized the anatomically oriented approach, which was only to be re-emphasized again by Ogden (1943), thus resulting in ambiguity concerning which approach yielded the better classification. The classifications mentioned all predated the availability of reliable chromosomal data, hence the systematic value of chromosome number in *Potamogeton* has not been evaluated.

The first known publication of a chromosome number for any *Potamogeton* was by Wiegand (1899) for *P. foliosus*, although Palmgren (1939) erroneously cited an earlier paper by Wiegand (1898) as containing the first counts for the genus. Other early chromosome number reports for *Potamogeton* were made by Wisniewska (1931) and Kuleszanka (1934) but the first such study of any magnitude was by Palmgren (1939) and included counts for 18 species. Published counts remained relatively scarce throughout the 1940's as evidenced by Ogden's (1943) remarks. According to Goldblatt (1979), 66 species of Potamogetonaceae had published counts available, which accounted for approximately 74% of the species. Because a substantial percentage of counts for species is now available in the literature, the use of chromosome numbers to assist formulation of systematic relationships within *Potamogeton* is feasible. Additionally, replicate counts published for the same taxa assist in evaluating the credibility of a given chromosome number report.

Incorporation of chromosome counts has facilitated progress in the phylogenetic reconstruction of other genera, but this technique has not yet so been used for *Potamogeton*. Stern (1961, p. 414) stated, "...reported chromosome numbers indicate that a thorough

cytotaxonomic investigation of [*Potamogeton*]. . .should yield interesting results, and would be a valuable adjunct to the previous extensive morphological and anatomical studies. . ."

The purpose of this paper is to bring together chromosome number reports from the literature and to discuss them in the context of taxonomic and phylogenetic relationships within *Potamogeton*.

METHODS

A compilation of chromosome number reports published for *Potamogeton* was made from data available in the following sources: Bolkhovskikh, et al, (1969), Cave (1958–1965), Darlington & Wylie (1956), Goldblatt (1981), Löve & Löve (1974; 1975), Moore (1970–74; 1977), and Ornduff (1967–69). Morphological descriptions were located for each species for which counts were available. The descriptions were compiled from recent floristic treatments.

Synonomy is an important issue regarding how counts are best apportioned to taxa. It is recognized that the author's allocation of chromosome counts to a taxon identified as a particular species may not be in accord with some opinions. Most of the discrepancy appears to involve nomenclatural issues, however, and as such does not create a problem in terms of to which taxon a particular count should be assigned. Because of the scope of this study, however, no attempts were made to obtain verified voucher specimens which correspond with the chromosome counts reported in the literature. For the most part, synonomy presented in major floristic works was followed assuming that such works reflect the input of taxonomic expertise.

The author is also aware of controversy regarding constitution of adequate methodology for conclusively recognizing hybrids in this genus and makes no claim of possessing the ability to ascertain correctly which taxa represent hybrids and which represent "pure" species. Therefore, the decision was made to eliminate "questionable" taxa (*i.e.*, those taxa widely considered to represent sterile hybrids) from further consideration in this study.

Species names which the author accepts to represent the correct nomenclature and which are not thought to be sterile hybrids are listed in Table 1 along with the corresponding $2n$ chromosome numbers and numbers of studies corroborating each count. Names not appearing in Table 1 (and for which counts are reported) are

listed in Table 2 along with reasons for their exclusion. The morphological descriptions of the species given in Table 1 were used to construct Table 3. Morphological groups in Table 3 were delimited on the basis of the author's perspective of general morphological groups occurring in *Potamogeton*. The groups divide linear-leaved species from broad-leaved species and further separate taxa on the basis of other leaf and stipule characters. In itself, Table 3 is not meant to infer taxonomic affinities between or among taxa. The classification followed in Table 4 is that of Hagström (1916), modified only to include species described after completion of that work. The $2n$ chromosome numbers are those from Table 1. The morphological groups (A–F) are from Table 3. Fruit types, either smooth (S) or keeled (K) were designated for each species. The smooth type refers to fruits in which the dorsal keel is absent or greatly reduced, whereas the keeled fruits possess prominent dorsal keels. The assignments of fruit types were made based upon descriptions given in the following references: Aalto (1970; 1974) Komarov (1937), Ogden (1953), and Ohwi (1965). Species for which the fruit type is unknown are designated by a question mark (?).

RESULTS AND DISCUSSION

Upon examination of Table 1, six discrete ploidy levels can be detected. It is further evident that the genus is characterized by two different euploid series, one based upon $x = 7$ and the other upon $x = 13$ as previously noted by Harada (1956).

In Table 3 a correlation can be noted between chromosome numbers and the six morphological groups selected to characterize the genus. Most of the groups are dominated by one ploidy level, or at least by one of the two euploid series, which suggests a relationship between ploidy levels and general morphology of the species. Groups A and D are conspicuous exceptions because mixtures of both ploidy levels and euploid series occur. It is noteworthy that floating-leaved species occur in both of the euploid series, including the lowest levels for each (*i.e.*, $2n = 26$; 28). Furthermore, floating leaves are also produced by *P. illinoensis* which has the highest chromosome number known for any species of *Potamogeton*.

In Table 4, a comparison of species from an anatomical standpoint is given, *i.e.*, essentially the Hagström classification. Superimposed on this classification are chromosome number, morpho-

Table 1. **2*n* Chromosome numbers of *Potamogeton* species incorporated into this study**
(number of concurring references for count is given in parentheses)

Species	2*n*		Species	2*n*	
P. acutifolius	26	(2)	P. nipponicus	52	(1)
P. alpinus	52	(6)	P. nodosus	52	(3)
P. amplifolius	52	(1)	P. oblongus	26	(2)
P. asiaticus	28	(1)	P. obtusifolius	26	(1)
P. coloratus	26	(1)	P. octandrus	28	(4)
P. crispus	52	(9)	P. orientalis	28	(1)
P. cristatus	28	(2)	P. oxyphyllus	26	(1)
P. dentatus	52	(2)	P. pectinatus	78	(9)
P. distinctus	52	(2)	P. perfoliatus	52	(12)
P. epihydrus	26	(2)	P. polygonifolius	52	(2)
P. filiformis	78	(6)	P. praelongus	52	(6)
P. foliosus	28	(1)	P. pusillus	26	(6)
P. franchetti	52	(1)	P. richardsonii	52	(3)
P. friesii	26	(2)	P. robinsii	52	(1)
P. fryeri	42	(4)	P. rutilus	26	(1)
P. gramineus	52	(8)	P. sibiricus	28	(1)
P. groenlandicus	26	(1)	P. strictifolius	52	(1)
P. illinoensis	104	(2)	P. trichoides	26	(3)
P. lucens	52	(2)	P. vaginatus	78	(4)
P. maackianus	52	(2)	P. vaseyi	28	(1)
P. malaianus	52	(2)	P. zosterifolius	26	(3)
P. natans	52	(8)	P. zosteriformis	52	(1)

TOTAL: 44 species

logical group and fruit type for each listed taxon. High concordance of chromosome numbers, morphological groups and fruit types is evident in the subgenus *Coleogeton*, the section *Adnati*, and the subsections *Compressi*, *Lucentes*, *Perfoliati*, *Javanici*, and *Colorati*. Considerable heterogeneity of these features, however, is notable in subsections *Pusilli*, *Oxyphylli*, and *Amplifolii*. Species of the $x = 13$ chromosomal series possess both keeled and smooth fruits, whereas species of the $x = 7$ series have only keeled fruits (the latter type being more prevalent in the genus). More $x = 13$ species in group A

Table 2. **Disposition of problematic species having published counts**

Species	**Disposition**
P. alatus	= P. distinctus*
P. anguillanus	excluded (lack of adequate description)
P. apertus	excluded (alleged hybrid)
P. berchtholdii	= P. pusillus*
P. biwaensis	excluded (alleged hybrid)
P. compressus	= P. zosterifolius*
P. densus	excluded (= Groenlandia densa)
P. faurieri	excluded (alleged hybrid)
P. flabellatus	= P. pectinatus*
P. fluitans	exluded (alleged hybrid)
P. indicus	= P. nodosus*
P. kamogawaensis	excluded (alleged hybrid)
P. leptocephalus	excluded (alleged hybrid)
P. limosellifolius	= P. octandrus*
P. longipetiolatus	= P. distinctus*
P. malainoides	excluded (alleged hybrid)
P. miduhikimo	= P. octandrus*
P. miyakezimaensis	= P. malaianus*
P. monoginous	= P. trichoides*
P. morongii	= P. natans*
P. numsakianus	= P. octandrus*
P. panormitanus	= P. pusillus*
P. porsiaticus	excluded (lack of adequate description)
P. subfluitans	excluded (lack of adequate description)
P. subsessilifolius	= P. fryeri*
P. teganumensis	= P. dentatus*
P. tenuifolius	= P. maackianus*
P. tepperi	= P. franchetii*
P. torquatus	= P. fryeri*

TOTAL: 29 species

*Counts published under the respective problematic names were applied to these synonyms

(linear-leaved species) have smooth fruits than keeled fruits; this relationship being particularly discernible in subsection *Pusilli*. These chromosome number discrepancies indicate the need for a re-evaluation of portions of the Hagström classification.

The suggestion that morphological groups within the genus may each correlate with a different ploidy level has been made by Haynes (1974). Attempts to arrive at correlations between ploidy and morphology have led to conflicting hypotheses. An example is the question of whether species of *Potamogeton* possessing floating leaves are more primitive than their strictly submersed-leaved counterparts. Chrysler (1907, p. 183) considered the floating-leaved species to be more primitive than the submersed-leaved species, which he believed to have been derived from the former as "...a stage in the assumption of the aquatic life by the genus." He further believed that *Potamogeton* evolved from a terrestrial ancestor, the classical interpretation applied to most aquatic plants by Arber (1920), Sculthorpe (1967), and others. Cronquist (1968; 1981), however, considers *Potamogeton* to have evolved from an aquatic ancestor likely related to the dicotyledon order Nymphaeales. Haynes (1974) agreed with Cronquist and formulated a hypothesis of evolutionary progression in *Potamogeton* contradictory to the classical viewpoint. He (p. 582) invoked the "phyllode theory" (Candolle, 1827; Arber, 1920) for explaining the evolution of leaf morphology in the genus: "...one could infer that the floating leaves might have been derived from the submersed leaves by an increase in the amount of tissue between the veins near the tip of the petiole. This would imply that possibly the floating-leaved species were derived from some ancestral stock of submersed-leaved plants." Haynes supported his hypothesis with cytological data which indicated (p. 582) "The submersed-leaved species are, for the most part, diploid, whereas the floating-leaved species are, for the most part, tetraploid." His conclusion was that cytological data indicated (p. 583) "...the primitive condition probably was that of total vegetative submergence." Haynes also used chromosome numbers to support his contention that anemophily is primitive in *Potamogeton* while hydrophily is derived due to the occurrence of the latter mechanism only in species characterized by high chromosome numbers while anemophilous species were characterized by lower chromosome numbers. Although the above arguments are reasonable, there

Table 3. **Basic morphological types in Potamogeton**

I. Floating leaves absent; submersed leaves various

A. Submersed leaves linear, stipules free (Group A)

1.	P. acutifolius	(26)
2.	P. foliosus	(28)
3.	P. friesii	(26)
4.	P. groenlandicus	(26)
5.	P. obtusifolius	(26)
6.	P. orientalis	(28)
7.	P. oxyphyllus	(26)
8.	P. pusillus	(26)
9.	P. rutilus	(26)
10.	P. sibiricus	(28)
11.	P. strictifolius	(52)
12.	P. trichoides	(26)
13.	P. zosterifolius	(26)
14.	P. zosteriformis	(52)

B. Submersed leaves broad, stipules free (Group B)

1.	P. crispus	(52)
2.	P. dentatus	(52)
3.	P. lucens	(52)
4.	P. malaianus	(52)
5.	P. perfoliatus	(52)
6.	P. praelongus	(52)
7.	P. richardsonii	(52)

C. Submersed leaves linear, stipules fused (Group C)

1.	P. filiformis	(78)
2.	P. pectinatus	(78)
3.	P. robbinsii	(52)
4.	P. vaginatus	(78)

II. Floating leaves present; submersed leaves various

D. Submersed leaves linear, stipules free (Group D)

1.	P. asiaticus	(28)
2.	P. cristatus	(28)
3.	P. epihydrus	(26)
4.	P. natans	(52)
5.	P. octandrus	(28)
6.	P. vaseyi	(28)

E. Submersed leaves linear, stipules fused (Group E)

1.	P. maackianus	(52)

F. Submersed leaves broad, stipules free (Group F)

1.	P. alpinus	(52)
2.	P. amplifolius	(52)
3.	P. coloratus	(26)
4.	P. distinctus	(52)
5.	P. franchetii	(52)
6.	P. fryeri	(42)
7.	P. gramineus	(52)
8.	P. illinoensis	(104)
9.	P. nipponicus	(52)
10.	P. nodosus	(52)
11.	P. oblongus	(26)
12.	P. polygonifolius	(52)

( ) denotes $2n$ chromosome number for Table 1.

is still a discrepancy from an adaptive standpoint. If wind pollination is primitive, then why should the primitive state be characterized by total vegetative submergence, and if water-pollinated species are advanced, then why do they all lack floating leaves?

Ths Significance of Aneuploidy

Curiously, the presence of two chromosomal series within *Potamogeton* has not lead to a re-appraisal of systematic relationships among the species despite the fact it has been realized since the 1950's (Harada, 1956) and is still currently emphasized (*e.g.*, Grant, 1982). From a systematic standpoint, it would be highly desirable to know whether each line represents a monophyletic assemblage. If this indeed apears to be the case, then the classification of the genus should reflect consistent segregation of species from the separate lineages, *i.e.*, no one group should include species from both chromosomal series if a natural arrangement is to be depicted.

Investigators usually regard the euploid series based upon $x = 13$ as typical for the genus, and treat species possessing chromosome numbers of 28 or 42 as "anomalous." An example of this approach is illustrated by Haynes' (1974) treatment of subsection *Pusilli* in which he hypothesized that *P. foliosus* ($2n = 28$) was derived from a $2n = 26$ progenitor by aneuploidy. Since the other species within the subsection possess chromosome numbers based upon $x = 13$, his interpretation would appear reasonable. However, the more widespread occurrence of the $2n = 28$ species must be considered. The presence of $2n = 28$ species within the subsections *Oxyphylli* and *Javanici* (the former also including $2n = 26$ species) would imply that aneuploidy had originated independently at least two separate times in the genus, or that the subsections are not natural. All counted species within subsection *Javanici* are $2n = 28$ which implies that a single "aneuploid" event may have originated that group, but the progenitor of *Javanici* would have had to arise from a $2n = 28$ species in another subsection, or from a $2n = 26$ species by yet another aneuploid event. Furthermore, there is the questionable presence of *P. fryeri* ($2n = 42$) in a subsection characterized by $2n = 52$ species. The "anomaly" would have to be explained by still another aneuploid event in the $2n = 26$ progenitor of the group. It is unlikely, therefore, that recurring aneuploidy reasonably explains

Table 4. Relationships of chromosome numbers and morphology to sub-generic ranks (see text for explanation of symbols)

	2*n*	morphological group	fruit type
I. Subgenus: *Coleogeton*			
1. Section: *Connati*			
a. Subsection: *Filiformes*			
1. *P. filiformis*	78	C	S
2. Section: *Convoluti*			
a. Subsection: *Vaginati*			
1. *P. vaginatus*	78	C	S
b. Subsection: *Pectinati*			
1. *P. pectinatus*	78	C	S
II. Subgenus: *Potamogeton*			
1. Section: *Adnati*			
a. Subsection: *Serrulati*			
1. *P. robbinsii*	52	C	K
2. *P. maackianus*	52	E	K
2. Section: *Axillares*			
a. Subsection: *Pusilli*			
1. *P. foliosus*	28	A	K
2. *P. orientalis*	28	A	?
3. *P. obtusifolius*	26	A	S
4. *P. pusillus*	26	A	S
5. *P. friesii*	26	A	S
6. *P. rutilus*	26	A	S
7. *P. groenlandicus*	26	A	?
8. *P. strictifolius*	52	A	S
f. Subsection: *Lucentes*			
1. *P. lucens*	52	B	K
2. *P. dentatus*	52	B	K
3. *P. malaianus*	52	B	K
4. *P. distinctus*	52	F	K
5. *P. gramineus*	52	F	K
6. *P. nipponicus*	52	F	?
7. *P. illinoensis*	104	F	K
g. Subsection: *Praelongi*			
1. *P. praelongus*	52	B	K
h. Subsection: *Perfoliati*			
1. *P. perfoliatus*	52	B	S
2. *P. richardsonii*	52	B	S
i. Subsection: *Javanici*			
1. *P. asiaticus*	28	D	K
2. *P. cristatus*	28	D	K
3. *P. octandrus*	28	D	K
4. *P. vaseyi*	28	D	K
j. Subsection: *Amplifolii*			
1. *P. amplifolius*	52	F	S
2. *P. franchetii*	52	F	K
3. *P. fryeri*	42	F	K
k. Subsection: *Natantes*			
1. *P. natans*	52	D	S
l. Subsection: *Hybridi*			

b. Subsection: *Monogyni*			
1. *P. trichoides*	26	A	K
c. Subsection: *Compressi*			
1. *P. acutifolius*	26	A	K
2. *P. zosterifolius*	26	A	K
3. *P. zosteriformis*	52	A	K
d. Subsection: *Oxyphylli*			
1. *P. sibiricus*	28	A	K
2. *P. oxyphyllus*	26	A	S
e. Subsection: *Crispi*			
1. *P. crispus*	52	B	S
1. *P. epiphydrus*	26	D	K
m. Subsection: *Colorati*			
1. *P. coloratus*	26	F	S
2. *P. oblongus*	26	F	S
3. *P. polygonifolius*	52	F	S
n. Subsection: *Alpini*			
1. *P. alpinus*	52	F	K
o. Subsection: *Nodosi*			
1. *P. nodosus*	52	F	K

the origin of $2n = 28$ species. It is more likely that the $2n = 28$ species are monophyletic, have resulted from a single aneuploid event and have been simply misplaced throughout portions of the classification.

The question of the ancestral diploid number of the genus must be considered. Previous investigators (Stern, 1961; Haynes, 1974) have interpreted the chromosome numbers of $2n = 26$ or 28 to represent the diploid level in *Potamogeton*. Goldblatt (1979), however, suggested that in *Potamogetonaceae*, the base number is likely to be $x = 7$ and, therefore, all counted species of *Potamogeton* having $2n$ chromosome numbers exceeding 14 would indicate polyploidy. This interpretation is in accord with Grant (1963) and Stebbins (1971), who believe that haploid numbers in excess of $n = 10$–13 are indicative of polyploidy. The suggestion of Ehrendorfer et al. (1968) that the progenitors of the angiosperms were characterized by a base number of $x = 7$ may also be pertinent. Since *Potamogeton* is usually placed within the relatively primitive subclass Alismatidae (Cronquist, 1981; Takhtajan, 1969), it is conceivable that the base number for the genus would be $x = 7$. Evidence exists to support this interpretation. Four concurring studies have reported the chromosome number of *P. fryeri* to be $2n = 42$ (see Table 1). If $2n = 28$ is accepted as the diploid level, then *P. fryeri* would represent a triploid organism. If, however, $2n = 14$ is accepted as the diploid level, then *P. fryeri* would represent a hexaploid (while $2n = 28$ species would represent tetraploids). The latter interpretation is here accepted to be more reasonable.

Initially it was presumed that diploid ($2n = 14$) ancestors of the genus were extinct because counts of $2n = 14$ for any species of *Potamogeton* were absent from the literature. There is some indication to the contrary. A study by Wiegand (1899) reported the chromosome number of *P. foliosus* as $2n = 14$. The credibility of that report may well be questioned on the basis of whether an appropriate methodology was employed in that study. Early studies of chromosome numbers were often hampered by the use of sectioning methods (which Wiegand also used) that frequently resulted in overlooked chromosomes, but indications are that Wiegand's counts were probably accurate. It is unlikely, even by sectioning, that he would have missed half (13–14) of the chromosomes, especially since he reported the same number in his replicate counts. His illus-

trations clearly depict a chromosome number of $2n = 14$. Most convincing is the observation that Wiegand's count of $2n = 14$ is in accord with the chromosomal series to which *P. foliosus* belongs ($x = 7$). Since only two North American species are known to belong to that series, it is difficult to believe that inaccuracy on Wiegand's part would result in a count which was "coincidentally" within the proper numerical series. If the count of $2n = 14$ for *P. foliosus* is accepted as accurate, then it is evident that some species of *Potamogeton* may be characterized by different ploidy levels. As Tomlinson (1982) indicated, no cytological survey of large populations of a species has been conducted tor *Potamogeton* which could clarify this point.

The diploid level of *Potamogeton* is therefore recognized to be $2n = 14$. From this assumption follows that $x = 13$ species were derived from a $2n = 14$ diploid by descending aneuploidy. Aneuploid reduction is favored over the hypothesis of aneuploid addition to explain the patterns of chromosome number variation within *Potamogeton*. Stebbins (1966) stated that both polyploidy and aneuploid reduction are characteristic of many outcrossing species which occupy pioneer habitats. Aneuploidy is often favored in pioneer habitats since the causative unequal reciprocal translocations tie linked adaptive gene complexes (Stebbins, 1974). The genus *Potamogeton* includes outcrossing species which frequently occupy pioneer habitats.

Correlates to the Precedence of the $x = 7$ Series

The hypothesis that the $x = 7$ lineage gave rise to the $x = 13$ species of *Potamogeton* can be evaluated by how well other factors correlate with it. One factor involves the place of origin of the species. On the basis of fossil evidence, Miki (1937) suggested that *Potamogeton* originated in oriental Asia. When the geographical distributions of extant $x = 7$ species are studied, an eastern Asian affinity becomes apparent. Six of the eight known $x = 7$ species occur in eastern Asia whereas the two remaining species are found in North America (see Table 5). The $x = 7$ species are absent from other regions (with exception of the wide-ranging *P. octandrus*), and overall they represent a fairly small portion of the total number of species of *Potamogeton*. On the basis of these observations, a reasonable interpretation of evolutionary progression can be formu-

Table 5.
Geographical distributions of $x = 7$ species of *Potamogeton*

Species	$2n$	Distribution	Reference
P. asiaticus	28	Manchuria, USSR	Komarov (1937)
P. cristatus	28	China, USSR, Korea, Formosa	Ohwi (1965)
P. octandrus	28	China, USSR, Korea, Formosa, India, Malaysia	Ohwi (1965)
P. orientalis	28	Japan, eastern Asia	Hagström (1916)
P. sibiricus	28	E. Siberia (endemic)	Komarov (1937)
P. fryeri	42	Japan, Korea	Ohwi (1965)
P. vaseyi	28	United States & Canada	Hellquist & Crow (1980)
P. foliosus	28	North America	Haynes (1974)

lated. The concentration of $x = 7$ species in eastern Asia is compatible with Miki's hypothesis that *Potamogeton* originated there if this lineage is considered to be primitive. It is probable that diploid ($2n = 14$) species occurred throughout eastern Asia and that some of them dispersed into North America, which would account for the few $x = 7$ species on the latter continent. The disjunction of $x = 7$ species in eastern Asia and temperate North America coincides with the same distributional pattern of other plant species known to occur in both regions (*e.g.*, Hara, 1972). According to Raven and Axlerod (1974), the migration of plants between North America and Eurasia has been relatively unimpeded throughout much of the evolutionary history of the flowering plants, allowing migration of species across the North Atlantic region until about 49 millions years BP. When or where the $x = 13$ lineage arose is undetermined, but these species were apparently more successful than their $x = 7$ counterparts as evidenced by the larger number and wider distributions of extant $x = 13$ species. The successful radiation of $x = 13$ species throughout most continents of the world makes tracing their precise origin difficult. The relative scarcity of $x = 7$ species which survive today may be due to unsuccessful competition with their $x = 13$ descendants. Indeed, the persistence of *P. foliosus* ($2n = 28$)

in North America may be a result of the species high tolerances for various ecological extremes. In comparing the sensitivity of common aquatic plants, Stuckey (1975, p. 29) listed *P. foliosus* as an "insensitive species with wide ecological tolerances" which has "remained the same or increased in abundance through time." The greater success of $x = 13$ species is also evident from observations that this lineage includes higher level polyploids and is the only group possessing species exhibiting derived hydrophilous pollination (subgenus *Coleogeton*).

Fruit characters also reflect the ancestral nature of $x = 7$ species. Fruits of $x = 7$ species are prominently keeled (Table 4) whereas both keeled and keeless fruits occur among $x = 13$ species. The loss of keels appears restricted to the $x = 13$ lineage. Since keeled fruits occur within both chromosomal series, it is assumed that the keel represents the primitive condition. This interpretation is further supported by the occurrence of keeless fruits within subgenus *Coleogeton*. Subgenus *Coleogeton* is regarded as the most highly advanced group of the genus and the keeless fruits of the subgenus are interpreted to represent the derived state. Several species within subgenus *Potamogeton* possess fruits having small or highly reduced keels indicating a series of stages in the reduction of the structures.

Chromosome Numbers and Classification

The "working rank" in *Potamogeton* is the subsection and principal segregation of species occurs at this level. To be taxonomically meaningful, the subsections should represent monophyletic assemblages of species. An evaluation of constituent chromosome numbers is one method by which the naturalness of subsections of *Potamogeton* can be tested; however, a rationale for the analysis must be presented. In this genus, variation in chromosome number results from two processes — aneuploidy and polyploidy. As discussed above, it is probable that $x = 7$ represents the ancestral lineage. From this starting point are two possible explanations for the origin of aneuploid ($x = 13$) species. Figure 1 presents the two hypotheses. One possibility (single origin hypothesis) is that the $x = 13$ series originated by a single aneuploid event in which a $2n = 14$ diploid gave rise to a $2n = 13$ diploid which persisted by chromosomal doubling ($2n = 26$). The higher polyploids in the $x = 13$ series would have been derived from the $2n = 26$ tetraploids. In this

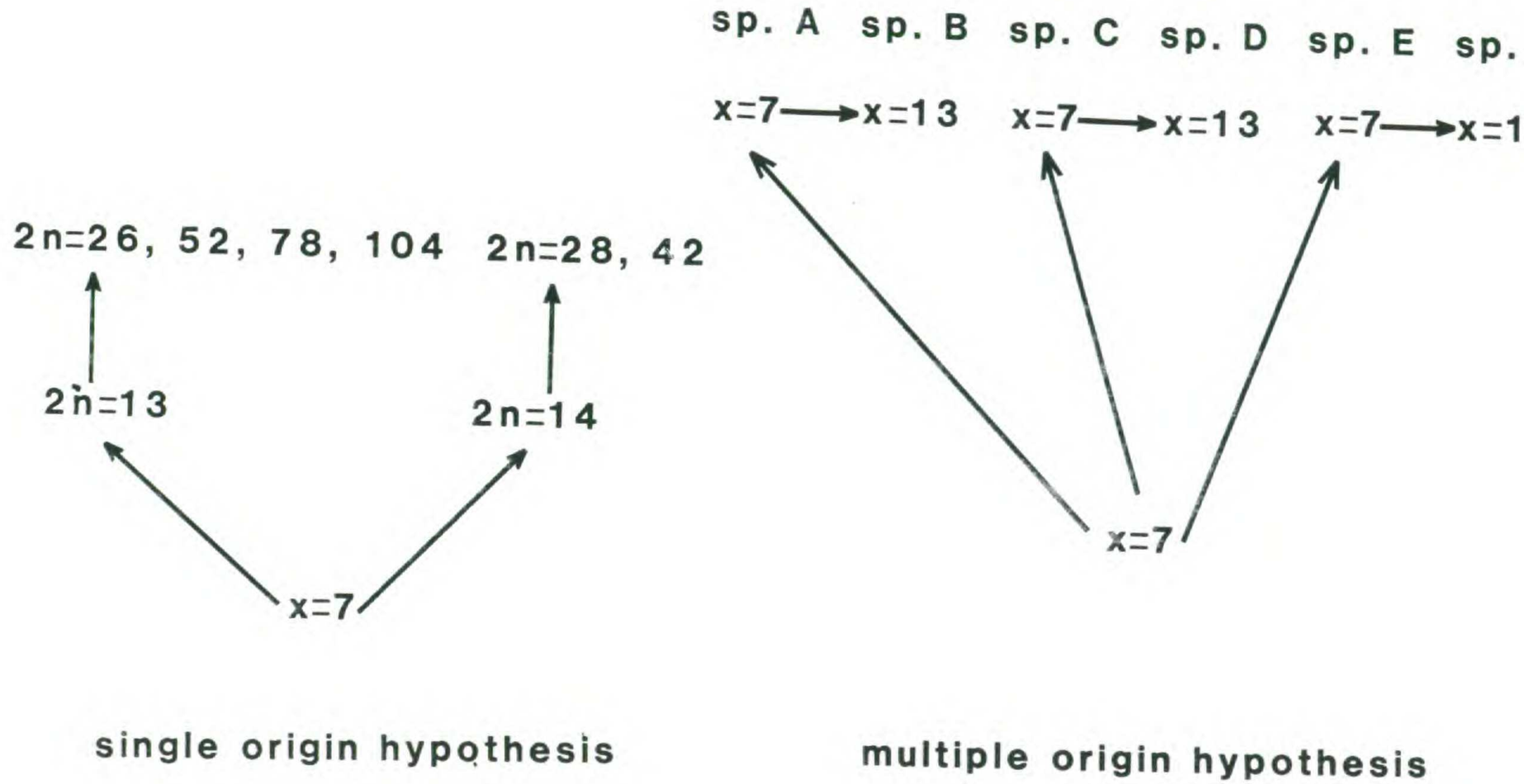

Figure 1. Hypothetical Origins of x = 13 Species

instance, the affinities between species would be greatest within the same numerical series and least between the two numerical series. In the second hypothesis, however, affinities could be much stronger between species in different series (*e.g.*, sp. A and sp. B) than between those in the same series (*e.g.*, sp. B and sp. F). If the aneuploid species arose from multiple origins, then one would expect the grouping of closely related species (such as represented by a subsection) to include members from both numerical series as well as from different ploidy levels. If aneuploid species arose from a single event, then the uniformity of subsections regarding both numerical series and ploidy levels would be expected. Referring back to Table 4, it is evident that the subsections reflect homogeneity in terms of both numerical series and ploidy levels of the constituents. This observation supports the single-origin hypothesis of aneuploid species. One difficulty in accepting this hypothesis is that subsections should be entirely characterized by species belonging to only one numerical series ($x = 7$ or $x = 13$). Although this is generally true for the representatives surveyed in this study, there are exceptions. In subsections *Pusilli, Oxyphylli* and *Amplifolii* occur species from both $x = 7$ and $x = 13$ series. This discrepancy suggests a misalignment of species. On the basis of anatomy and inflorescence characters, both subsection *Pusilli* and subsection *Oxyphylli* were noted by Hagström (1916) to be closely related to subsection *Javanici,* the only subsection comprised entirely of $x = 7$ species. It is probable, therefore, that the $x = 7$ species in subsection *Pusilli (P. foliosus* and *P. orientalis)* along with *P. sibiricus* from subsection *Oxyphylli* should rightfully be placed within or close to subsection *Javanici* instead of in their present situation. Such an adjustment would also result in a greater uniformity of fruit types within the subsections. *Potamogeton foliosus, P. orientalis* and *P. sibiricus* are also geographically related (Table 5). Likewise, the removal of *P. fryeri* from subsection *Amplifolii* may also be warranted. This species may represent a highly advanced member of subsection *Javanici* or could also be placed close to that subsection. Naturally, more detailed comparative work is needed before such taxonomic decisions can be fully justified.

With regard to polyploidy, most subsections appear to be characterized by one ploidy level, although there are a number of instances where a subsection will also include a species which is at a higher

ploidy level (*e.g.*, subsections *Pusilli, Compressi, Lucentes, Colorati*). In such situations, chromosome number alone cannot provide sufficient evidence for determining the evolutionary relationships among species. Perhaps a comparative analysis of somatic karyotypes, banding, etc., would be more revealing than simple comparisons of numbers. Because higher polyploids occur infrequently in a subsection and yet are found in various subsections, it is likely that polyploidy has occurred independently in divergent lines of $2n = 26$ species thus producing hexaploids and higher levels. In such instances, a higher level polyploid may represent an advanced member of a particular group. It is also unlikely that certain species represent transitional ploidy levels in a continuum from $2n = 26$ to $2n = 52$, 78, or 104 species, and thus could tie together phylogenetically certain subsections which are characterized by these ploidy levels. There is the question of whether a particular ploidy level (*e.g.*, $2n = 52$) has resulted from one polyploid event or from parallel polyploidy arising in divergent groups. A satisfactory elucidation of the problem may be better achieved as a result of biochemical, cytogenetic, and hybridization studies.

St. John's (1916) revision of section *Coleophylli* appeared concurrently with Hagström's (1916) monograph of *Potamogeton*. Interestingly, St. John considered *P. filiformis, P. pectinatus,* and *P. vaginatus* (as *P. moniliformis*) to belong to a single section *(Coleophylli),* whereas Hagström viewed each species as belonging to different subsections, and further divided those into two sections (*Connati* and *Convoluti*). St. John also differed from Hagström by including *P. robbinsii* in section *Coleophylli* while Hagström considered the species to belong in a different subgenus (*Potamogeton)* in section *Adnati. Potamogeton filiformis, P. pectinatus,* and *P. vaginatus* have identical chromosome numbers ($2n = 78$) which differ from that of *P. robbinsii* ($2n = 52$). *P. robbinsii* also differs from the three aforementioned species by its keeled fruit, lack of hypodermis, and presence of mechanical tissue in the peduncle (Hagström, 1916). In this respect, Hagström's inclusion of *P. robbinsii* in subgenus *Potamogeton* may be justified. On the other hand, St. John's combination of *P. filiformis, P. pectinatus* and *P. vaginatus* into one section is supported by the agreement of chromosome number, morphology and fruit type of these species.

Floating-leaved Species – Primitive or Advanced?

As previously mentioned, correlations have been attempted between chromosome numbers and the presence of floating leaves. A perspective of the problem developed by examining a larger group of species fails to substantiate this correlation. The lowest representative ploidy level at which to make such a comparison is tetraploid ($2n = 26$ or 28). At the tetraploid level, some species in each chromosomal series have floating leaves whereas others have only submersed leaves, thus presenting no clue to which morphological type arose first. Even the apparent loss of floating leaves in the advanced, high polyploid subgenus *Coleogeton* cannot be regarded as characteristic of high ploidy levels in general since floating leaves are still found at even higher ploidy levels (*e.g., P. illinoensis).* The primitiveness of floating leaves can be neither proven nor disproven solely on the basis of chromosome numbers, although other evidence may be brought to bear on the question. From an adaptive viewpoint, it is difficult to rationalize total vegetative submergence for an ancestor characterized by wind pollination. The arguments favoring an aquatic origin for *Potamogeton* have not been adequately substantiated although evidence for a terrestrial ancestry of the group is provided by Miki (1937) and den Hartog (1970). Miki believed *Potamogeton* to have originated from a different subclass (Arecidae) than is usually considered, *i.e.,* Alismatidae (Cronquist, 1981; Takhtajan, 1969), thereby destroying the "link" to the aquatic members of the Alismatidae. Den Hartog believed that marine representatives of *Potamogetonaceae* arose from terrestrial ancestors. If this is the case, then the freshwater *Potamogeton* are also likely to be of terrestrial ancestry. The more reasonable explanation still appears to be that *Potamogeton* originated with floating leaves as an intermediate stage between a terrestrial ancestry and adoption of the hydric habit. Also supporting this argument is the study by Kadono (1982) wherein the epistomatous nature of submersed and seedling leaves of several *Potamogeton* species suggested to him that submersed leaves arose from floating leaves, and that the genus possibly evolved from ancestors having floating leaves.

The appearance and disappearance of floating leaves throughout the genus is no doubt partially due to reversals. Although the genetic basis for heterophylly in *Potamogeton* is not well under-

stood, some support for this opinion exists. Heterophylly can be regulated in *P. nodosus* simply by varying the concentration of abscisic acid (Anderson, 1978) thus implying that the genetic mechanism responsible for controlling the foliar states is relatively simple. Thieret (1971) observed the production of floating leaves in *P. richardsonii* (a species that normally produces only submersed foliage) as an apparent response to dropping water levels. This changeover indicates that the genetic mechanism may still exist to produce floating leaves in species which were thought to have lost the ability to do so. Hagström (1916) apparently recognized convergence of floating-leaved species since he included both floating-leaved and submersed-leaved species within subsections on the basis of other overwhelming similarities (*e.g.*, subsections *Lucentes* and *Serrulati*).

CONCLUSIONS

A survey of chromosome numbers reported for species of *Potamogeton* has substantiated the view that the genus is characterized by two different polyploid series, one based upon $x = 7$ and the other upon $x = 13$. The diploid level of the genus is interpreted to be $2n = 14$. The $x = 13$ lineage is proposed to have arisen from one incidence of aneuploidy from a $2n = 14$ progenitor. Chromosome number data support the hypothesis that *Potamogeton* originated in Asia. A review of chromosome numbers indicates that subsections *Pusilli*, *Oxyphylli*, and *Amplifolii* may not represent entirely natural assemblages and it is suggested that a reconsideration of the classification of *Potamogeton* be made in order to accommodate discrepancies noted in regard to chromosome numbers and other features. Cytological investigations of large population samples of species are encouraged in order to obtain better insight into evolutionary processes occurring within the genus. Chromosome numbers cannot be used to directly demonstrate the primitiveness of floating leaves in the genus, although it is believed that additional evidence supports this view. Available evidence suggests a different overview of evolutionary patterns in this genus than has been previously made. Hopefully, a complete synthesis of morphological, anatomical, cytogenetic, biochemical and other data will eventually enable a more accurate phylogenetic reconstruction of *Potamogeton* to be made and thus will provide systematists with the best classification to use for this genus.

ACKNOWLEDGMENTS

I would like to express my thanks to Dr. D. J. Crawford (The Ohio State University), Dr. R. R. Haynes (The University of Alabama) and Dr. R. L. Stuckey (The Ohio State University) for their helpful comments and suggestions for improving this manuscript.

LITERATURE CITED

AALTO, M. 1970. Potamogetonaceae fruits. I. Recent and subfossil endocarps of the Fennoscandian species. Acta Bot. Fenn. **88:** 1–85.

_____. 1974. Potamogetonaceae fruits. II. *Potamogeton robinnsii*, a seldom fruiting North American pondweed species. Ann. Bot. Fenn. **11:** 29–33.

ANDERSON, L. W. J. 1978. Abscisic acid induces formation of floating leaves in the heterophyllous aquatic angiosperm *Potamogeton nodosus*. Science **201:** 1135–1138.

ARBER, A. 1920. Water Plants: A Study of Aquatic Angiosperms. University Press, Cambridge, 436 pp.

ASCHERSON, P., & P. GRAEBNER. 1907. IV. II. Potamogetonaceae *In:* A. Engler. *Das Pflanzenreich*. Leipzig. Verlag von Wilhelm Engelmann. 184 pp.

BOLKHOVSKIKH, Z., ET AL. 1969. Chromosome Numbers of Flowering Plants [in Russian]. Acad. Sci. of the USSR, Leningrad. 926 pp.

CANDOLLE, AUGUSTE P. de. 1827. *Organographie Vegetale*. Vol. I, book 2, chapter 3. Paris.

CAVE, M. S., ed. 1958–1965. Index to plant chromosome numbers for 1956–1964. Index for the years 1956–57 published by California Botanical Society; Index for 1958–1964 published by the University of North Carolina Press, Chapel Hill. Index to plant chromosome numbers supplement (previous to 1956) published in 1959 by California Botanical Society.

CHRYSLER, M. A. 1907. The structure and the relationships of the Potamogetonaceae and allied families. Bot. Gaz. (Crawfordsville) **44:** 161–188.

COOK, C. D. K., B. J. GUT, E. M. RIX, J. SCHNELLER, & M. SEITZ. 1974. Water Plants of the World. W. Junk b.v., publishers, The Hague, The Netherlands. 561 pp.

CRONQUIST, A. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin Co., Boston. 396 pp.

_____. 1981. An Integrated System of Classification of Flowering Plants. Columbia University Press, New York. pp. 1031–1036.

DARLINGTON, C. D., & A. P. WYLIE. 1956. Chromosome Atlas of Flowering Plants. Macmillan Co., New York. p. 337.

EHRENDORFER, F., F. KRENDL, E. HABELER, & W. SAUER. 1968. Chromosome numbers and evolution in primitive angiosperms. Taxon **17:** 337–468.

FERNALD, M. L. 1932. The linear-leaved North American species of *Potamogeton* section *Axillares*. Mem. Amer. Acad. Arts. **17:** 1–183.

GOLDBLATT, P. 1979. Polyploidy in Angiosperms: Monocotyledons. *In:* W. H. Lewis, ed. Polyploidy: Biological Relevance. Plenum Press, New York. 583 pp.

_____. ed. 1981. Index to plant chromosome numbers 1975–1978. Monographs in Systematic Botany, Vol. **5.** Missouri Botanical Garden, St. Louis. 553 pp.

GRANT, V. 1963. The Origin of Adaptations. Columbia University Press, New York.

_____. 1982. Periodicities in the chromosome numbers of the angiosperms. Bot. Gaz. **143:** 379–389.

HAGSTRÖM, J. O. 1916. Critical researches on the Potamogetons. Kongl. Svenska Vetenskapsakad. Handl. **55:** 1–281.

HARA, H. 1972. Corresponding taxa in North America, Japan and the Himalayas. pp. 61–72, *In:* D. H. Valentine (ed.), Taxonomy, Phytogeography and Evolution. Academic Press, New York.

HARADA, I. 1956. Cytological studies in the Helobiae I. Chromosome idiograms and a list of chromosome numbers in seven families. Cytologia **21:** 306–328.

HARTOG, C. DEN. 1970. The Sea-grasses of the World. North-Holland Publishing Co., Amsterdam. 275 pp.

HAYNES, R. R. 1974. A revision of North American *Potamogeton* subsection *Pusilli* (Potamogetonaceae). Rhodora **76:** 564-649.

HELLQUIST, C. B., & G. E. CROW. 1980. Aquatic Vascular Plants of New England: Part 1. Zosteraceae, Potamogetonaceae, Zannichelliaceae, Najadaceae. New Hampshire Agr. Exp. Sta. Bull. **515.** 68 pp.

KADONO, Y. 1982. On the stoma found in leaves of seedlings of some *Potamogeton* species. J. Jap. Bot. **57:** 332–336.

KOMAROV, V. L., ed. 1937. Flora of the USSR (Translated from Russian in 1970 by Israel Program for Scientific Translations, Jerusalem). Vol. 1. National Science Foundation, Washington, D.C. 244 pp.

KULESZANKA, J. 1934. Rozwoz ziarn pylk u *Potamogeton fluitans.* Acta. Soc. Bot. Poloniae **11:** 457–462.

LÖVE, A. & D. LÖVE. 1974. Cytotaxonomical Atlas of the Slovenian Flora. Verlag von J. Cramer. pp. 32–36.

_____. 1975. Cytotaxonomical Atlas of the Arctic Flora. J. Cramer. In der A. R Ganter Verlag Kommanditgesellschaft. FL–9490 Vaduz. pp. 25–29.

MIKI, S. The origin of *Najas* and *Potamogeton*. Bot. Mag. **51:** 472–481.

MOORE, R. J., ed. 1970. Index to plant chromosome numbers for 1968. Regnum Veg. **68:** 16–17.

_____. 1971. Index to plant chromosome numbers for 1969. Regnum Veg. **77:** 7.

_____. 1972. Index to plant chromosome numbers for 1970. Regnum Veg. **84.**

_____. 1973. Index to plant chromosome numbers 1967–1971. Oostoek's Uitgeversmaatschappij B. V., Domstraat 5–13, Utrecht, Netherlands, pp. 47–48.

_____. 1974. Index to plant chromosome numbers for 1972. Regnum Veg. **91.**

_____. 1977. Index to plant chromosome numbers for 1973/74. Regnum Veg. **96:** 179.

OGDEN, E. C. 1943. The broad-leaved species of *Potamogeton*. Rhodora **45:** 57–105, 119–163, 171–214.

_____. 1953. Key to the North American species of *Potamogeton*. New York State Museum Circular **31,** Albany. 11 pp.

OHWI, J. 1965. Flora of Japan. Smithsonian Institution, Washington, D.C. 1067 pp.

ORNDUFF, R., ed. 1957. Index to plant chromosome numbers for 1965. Regnum Veg. **50.**

_____. 1968. Index to plant chromosome numbers for 1966. Regnum Veg. **55:** 13.
_____. 1969. Index to plant chromosome numbers for 1967. Regnum Veg. **59:** 19.
PALMGREN, O. 1939. Cytological studies in *Potamogeton*. Bot. Not. **1939:** 246–248.
RAUNKIAER, C. 1895–99. *De danske blomsterplanters naturhistorie*. Bd. I. Enkimbladede. Copenhagen. 724 pp.
RAVEN, P. H., & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. **61:** 539–673.
SCULTHORPE, C. D. 1967. The Biology of Aquatic Vascular Plants. Edward Arnold, London. 610 pp.
ST. JOHN, H. 1916. A revision of the North American species of *Potamogeton* of the section *Coleophylli*. Rhodora **18:** 121–138.
_____. 1925. A critical consideration of Hagström's work on *Potamogeton*. Bull. Torrey Bot. Club **52:** 461–471.
STEBBINS, G. L. 1966. Chromosomal evolution and variation. Science **153:** 1463–1469.
_____. 1971. Chromosomal Evolution in Higher Plants. Edward Arnold, London. 216 pp.
_____. 1974. Flowering Plants – Evolution Above the Species Level. Belknap Press of Harvard University Press, Cambridge. 399 pp.
STERN, K. R. 1961. Chromosome numbers in nine taxa of *Potamogeton*. Bull. Torrey Bot. Club **88:** 411–414.
STUCKEY, R. L. 1975. Submersed aquatic vascular plants as indicators of environmental quality. *In:* C. C. King and L. E. Elfner (eds.). Organisms and biological communities as indicators of environmental quality –a symposium. Ohio Biological Survey Informative Circular No. **8.** pp. 27–30.
TAKHTAJAN, A. 1969. Flowering Plants –Origin and Dispersal. Oliver and Boyd: Edinburgh. 310 pp.
THIERET, J. W. 1971. Observations on some aquatic plants in northwestern Minnesota. Michigan Bot. **10:** 117–124.
TOMLINSON, P. B. 1982. VII. Helobiae (Alismatidae) (including the seagrasses). *In:* C. R. Metcalfe, ed. Anatomy of the monocotyledons. Clarendon Press, Oxford. 522 pp.
WIEGAND, K. M. 1898. Notes on the embryology of *Potamogeton*. *In:* W. F. Ganong "Society for Plant Morphology and Physiology" report of the Ithaca meeting, December 28–29, 1897. Bot. Gaz. **25:** 116.
_____. 1899. The development of the microsporangium and microspores in *Convallaria* and *Potamogeton*. Bot. Gaz. **28:** 328–359.
WISNIEWSKA, E. 1931. Rozwoz ziarn pylku u *Potamogeton perfoliatus* L. Acta. Soc. Bot. Poloniae **8:** 157–174.

COLLEGE OF BIOLOGICAL SCIENCES
DEPARTMENT OF BOTANY, THE OHIO STATE UNIVERSITY
COLUMBUS, OHIO 43210